

PALEOENVIRONMENTAL CONTROLS ON *SKOLITHOS SERRATUS*: A CASE STUDY FROM THE LOWER CRETACEOUS OF THE SANFRANCISCANA BASIN

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Abstract: *Skolithos serratus* differs from other simple, vertical, unbranched trace fossils by its distinctive horizontal scratch marks arranged in a screw-like pattern attributed to tiger beetle larvae (*Cicindelidae*). Despite its diagnostic morphology and established tracemaker, this ichnospecies remains poorly documented, with only sparse occurrences in the geological record. In this study, we present a detailed analysis of *Skolithos serratus* from floodplain deposits of the Quiricó Formation (Sanfranciscana Basin, Brazil). Our results demonstrate colonization in low-energy environments characterized by periods of non-deposition and subaerial exposure. This indicates a tracemaker preference for exposed, well-drained fine sandy substrates associated with lowered water tables, conditions necessary for the complete development of larval stages. Furthermore, *Skolithos serratus* colonization occurred predominantly during late-stage substrate drainage, facilitated by organisms with appendages adapted for burrowing into firm substrates developed between aggradation cycles driven by autocyclic processes. We also highlight the striking disparity in the documentation of *S. serratus* compared to other *Skolithos* ichnospecies in fluvial environments. This discrepancy reflects niche specialization by the *S. serratus* tracemaker and the strong control exerted by substrate properties, as all recorded occurrences are restricted to fine-grained heterolithic deposits composed predominantly of fine sand and mud. Finally, we expand the paleobiogeographic distribution of *Cicindelidae* in South America, as well as the record of their Mesozoic occurrences.

Keywords: Continental ichnology; Quiricó Formation; Ichnotaxonomy; Bioturbation; Trace fossils

1. INTRODUCTION

The study of trace fossils has become a crucial tool for understanding paleoenvironmental dynamics in ancient ecosystems. Over the past decade, increasing ichnological research has focused on depositional fluvial systems, particularly floodplains, to elucidate colonization patterns, environmental controls, and temporal changes in biological diversity (Hasiotis 2007, Melchor *et al.* 2012, Genise 2016). Among trace fossils characteristic of fluvial deposits, *Skolithos* exhibits widespread occurrence in both channel and floodplain environments, commonly attributed to arachnids, coleopterans, bees, or annelids (Melchor *et al.* 2012, Sedorko *et al.* 2025). However, its simple architectural design (i.e., vertical, unbranched burrows oriented perpendicular to bedding [Buatois *et al.* 2017]) combined with the diversity of potential tracemakers constrains inferences regarding the producer and paleoenvironmental conditions.

Despite this difficulty, *Skolithos* can exhibit coating and scratch marks that allow the distinction of probable tracemakers and consequent ichnospecific attribution (e.g., Alpert 1974, Gregory *et al.* 2006, Knaust 2017, Nascimento & Netto 2019). An example is *Skolithos serratus*, which differs from other *Skolithos* ichnospecies by possessing scratch marks perpendicular to the axis of the tube in the inner wall of the burrow, giving the burrow a screw-like shape (e.g., Netto 2007, Nascimento & Netto 2019). Despite this distinctive morphology, the ichnospecies *S. serratus* has rarely been documented in the literature (Mángano *et al.* 1994, Netto 2007, Nascimento & Netto 2019), and its paleoenvironmental significance remains poorly constrained.

In this study, we describe *Skolithos serratus* in heterolithic deposits of the Quiricó Formation (Sanfranciscana Basin, Brazil), discussing its paleoenvironmental significance and the role

of substrate properties in the preservation of perpendicular scratch marks. The objectives of this study are to: (1) detail the morphology of *Skolithos serratus* to address their ichnotaxonomic characteristics; (2) discuss the influence of substrate characteristics in trace fossil preservation; (3) link the occurrence of *Skolithos serratus* to its paleoenvironmental context.

2. GEOLOGICAL SETTING

The Sanfranciscana Basin is an intracratonic sedimentary basin covering approximately 150,000 km² in central-eastern Brazil (Campos & Dardenne 1997, Sgarbi *et al.* 2001). The basin comprises two sub-basins: (i) the Abaeté Sub-Basin; and (ii) the Urucuia Sub-Basin. Located in the southern Sanfranciscana Basin, the Abaeté Sub-Basin preserves fluvial-aeolian successions of the Areado, Mata da Corda, and Urucuia Groups. The Areado Group consists of: (1) alluvial fan conglomerates (Abaeté Formation) with quartz-rich matrix and clast-supported fabrics, transitioning to (2) lacustrine deposits (Quiricó Formation) comprising rhythmically interbedded mudstones and sandstones (Sgarbi 2000, Maraschin *et al.* 2016, Mescolotti *et al.* 2019, Batezelli *et al.* 2024).

This study focuses on outcrops of the Quiricó Formation (Fig. 1). The basal portion of the Quiricó Formation is characterized by perennial lake facies locally interbedded with alluvial sediments from the Abaeté Formation, consisting primarily of mudstones, shales (locally containing microfossils), and siltstones, with subordinate fine to coarse-grained sandstones and massive carbonate mudstones (Kattah 1991, Sgarbi *et al.* 2001, Simplicio *et al.* 2016, Cardoso *et al.* 2022, Batezelli *et al.* 2024). The upper portion of the Quiricó Formation comprises playa lake deposits laterally adjacent to the aeolian and fluvial beds of the Três Barras Formation (Fragoso *et al.* 2011, Simplicio *et al.* 2016). These deposits consist of fine-grained sandstones with a muddy matrix, cross-stratification, chert lenses, and gypsum crystal molds (Campos & Dardenne 1997, Mescolotti 2015, Simplicio *et*

al. 2016). The Quiricó Formation occurs interdigitated with aeolian deposits of Três Barras Formation (Kattah & Koutsoukos 1992, Pessagno Jr. & Dias-Brito 1996, Carvalho &

Kattah 1998, Dias-Brito *et al.* 1999, Sgarbi 2000, Maraschin *et al.* 2016, Mescolotti *et al.* 2019).

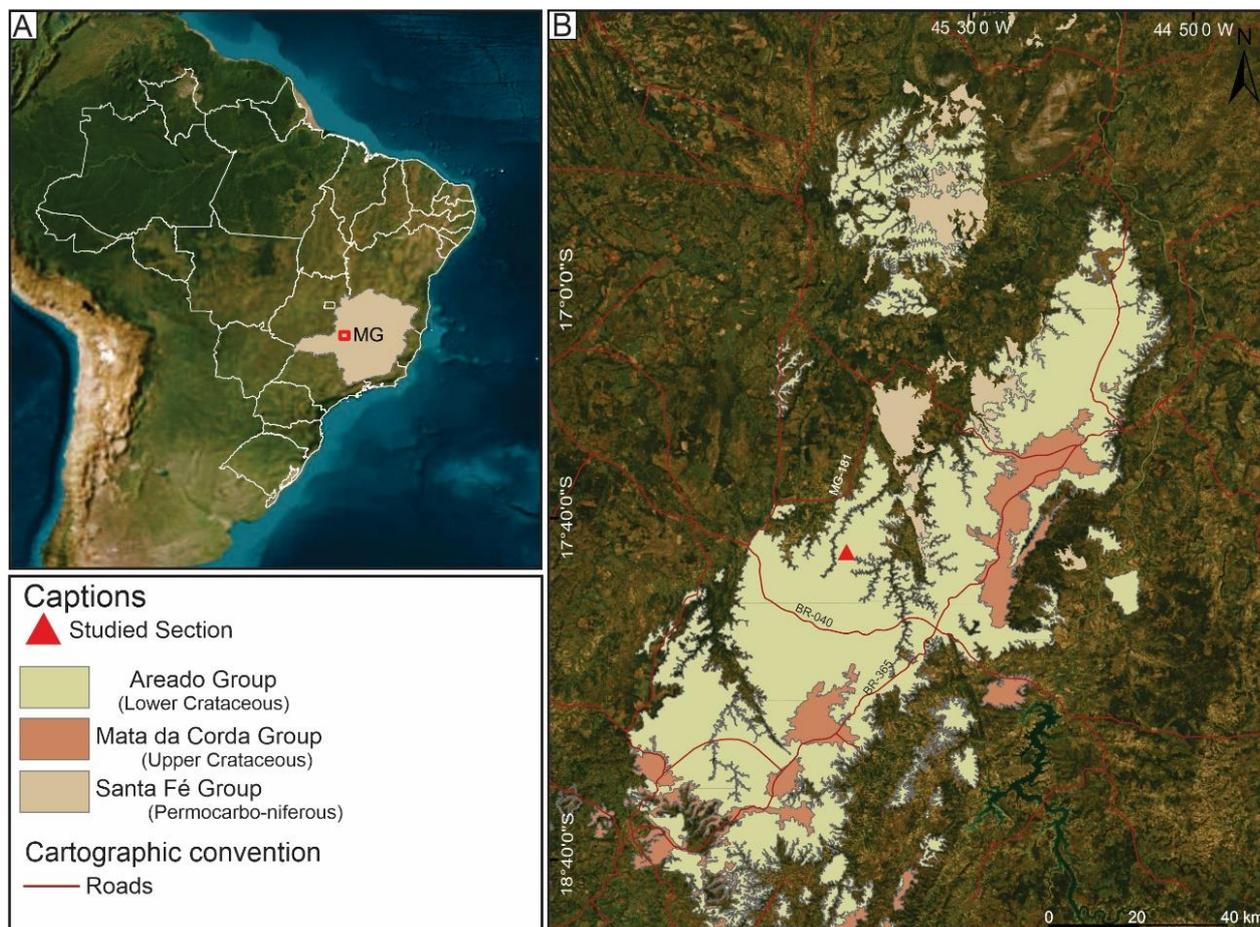


Figure 1 – Location map of studied section. A. Location of the study area (red square) in southeastern Brazil. B. Geological map of João Pinheiro region, highlighting the location of the studied section.

3. RESULTS

3.1. Sedimentary facies and depositional settings

The siliciclastic deposits in the study area exhibit planar-parallel laminations, with colors ranging from greenish to yellowish, forming tabular layers of fine to medium-grained siltstone. The ichnofossils identified as *Taenidium* and *Skolithos serratus* occur along an approximately 130 cm-thick interval preserved in these laminated heterolithic sandy-siltstones (Fig. 2A). The heterolithic deposits also include centimetric-thick lenticular fine-grained sandstone (Fig 2B),

interbedded with very fine to coarse-grained sandstone. Locally, these sandstones are conglomeratic and display through cross-stratification (Fig. 2C).

These deposits are interpreted as formed under perennial lacustrine environment. They occur at the base of the lacustrine system and indicate a low-energy deposition (Kattah 1991, Campos & Dardenne 1997, Sgarbi 2011, Simplicio *et al.* 2016, Cardoso *et al.* 2022). The lenticular sandstones interbedded within fine-grained lacustrine deposits suggest flows associated with flooding events (Bohacs *et al.* 2000).

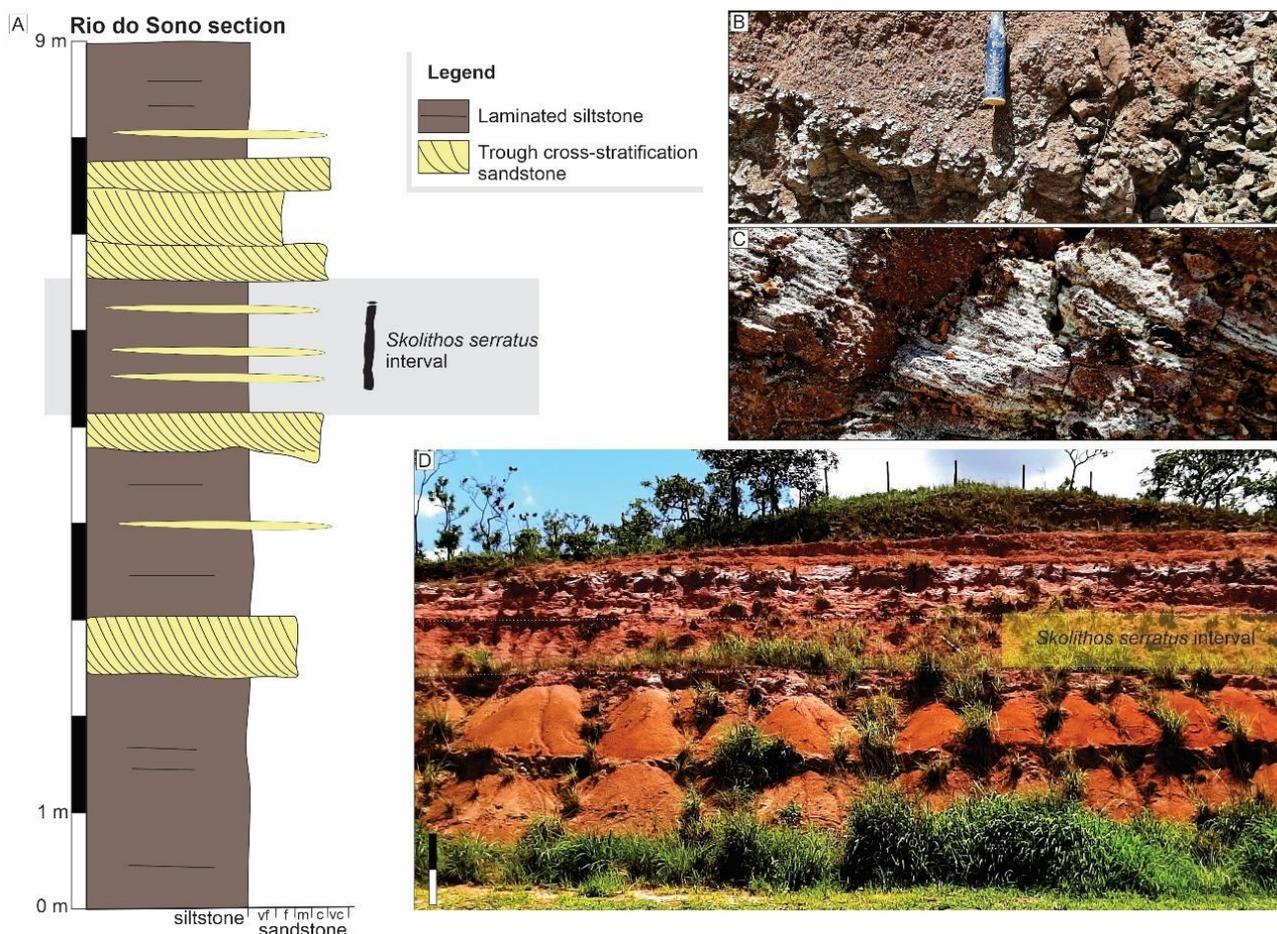


Figure 2 – Facies and sedimentologic log of studied section. A. Sedimentologic log highlighting the interval of occurrence of *Skolithos serratus* in the heterolithic laminated siltstone facies, attributed to Quiricó Formation. B. heterolithic siltstone facies. C. St facies. D. General view of studied outcrop, highlighting in yellow the interval rich in *Skolithos serratus* (scale bar = 2 m).

3.2. Trace fossil descriptions

Skolithos serratus Howell, 1957

Description: vertical to slightly inclined, unbranched burrows exhibiting irregular margins and a passive infill lithologically distinct from the host substrate. The inner burrow wall displays ornamentation consisting predominantly of horizontal scratches extending throughout the burrow length. The rings vary from 4 to 15 mm in thickness and are spaced 2 to 12 cm apart. The burrows show an average diameter of 7 mm and maximum

observed depth of 8.5 cm. The burrow walls exhibit irregular pattern with abrupt burrow-host rock contacts visible macroscopically.

Remarks: *Skolithos serratus* is distinguished from other *Skolithos* ichnospecies by its internal ornamentation: horizontally oriented scratches arranged perpendicular to the burrow axis, forming a screw-like pattern (Netto 2007, Nascimento & Netto 2019). *Skolithos serratus* is interpreted as the product of tiger beetle larvae (Cicindelidae) burrowing activity in well-drained, firm substrates (Nascimento & Netto 2019).

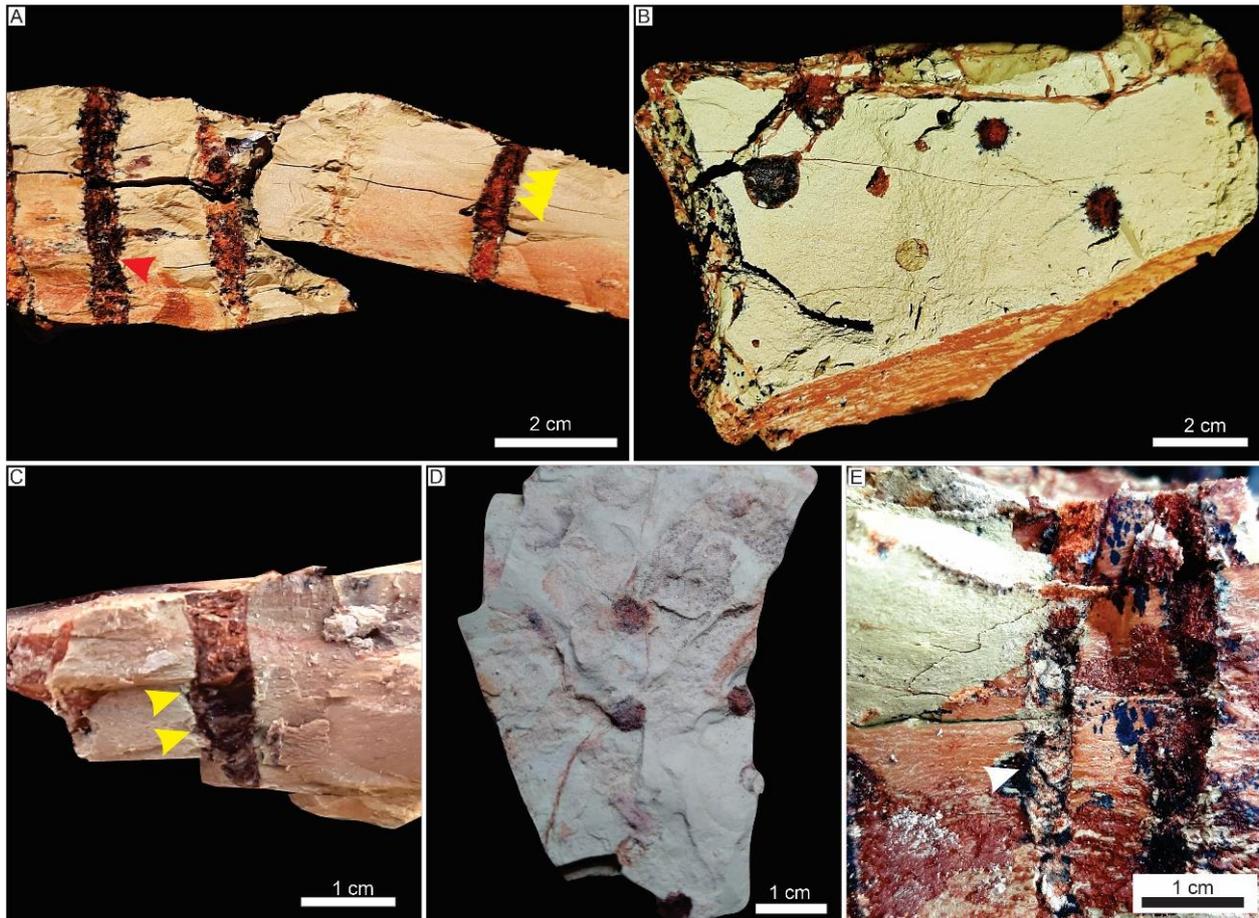


Figure 3 – Biogenic structures. A) *Skolithos serratus* in the vertical section, note the constraining of the burrows with abrupt contrast with the matrix (red arrow), and the crew-like pattern (yellow arrows). B) *Skolithos serratus* in the bedding plane view. C) and D) *Skolithos serratus* in siltstone, in cross section showing striated pattern in the inner burrow wall (yellow arrows). E) *Taenidium barretti* in siltstone with active meniscated infill (white arrow).

4. DISCUSSION

4.1. Paleoenvironmental significance

Skolithos serratus occurs in marginal lacustrine deposits of Quiricó Formation, indicating colonization of low-energy environments characterized by periods of non-deposition and subaerial exposure. Although classic sedimentologic signatures of subaerial exposure are absent (i.e. mudcracks), the presence of irregular walls and the filling of the burrows distinct from the matrix allow to interpret colonization of firm, exposed substrates. Thus, the tracemakers preferentially inhabited exposed, well-drained fine sandy substrates with lowered water tables, conditions essential for the complete development of most soil invertebrates with a larval stage (Genise 2016). Subaerial exposure and high evaporation rates due to semiarid conditions lead to progressive substrate

desiccation, transforming conditions from softground to firmground (Buatois & Mángano 2007). In this sense, *Skolithos serratus* colonization occurred primarily during later stages of soil drainage by organisms possessing appendages capable of burrowing in firm substrates, as observed in tiger beetle larvae (Brust *et al.* 2010). These inferences align with Netto (2007), who demonstrated that colonization by tracemaker of *S. serratus* occurred during specific windows between aggradation cycles triggered by autocyclic processes. Additionally, the *S. serratus* in this sedimentary context suggests that adult beetles selected these exposed areas as oviposition sites (Nascimento & Netto 2019). The ichnotaxon *Skolithos serratus* represents permanent dwellings for the tracemaker during its three larval stages and pupal stage. These burrows also served as a platform from which larvae ambush prey at the soil surface

(Nascimento & Netto 2019). The tiger beetle larvae exhibit an ambush predation strategy, positioning itself at the burrow entrance to stalk prey (Knisley & Schultz 1997, Brust *et al.* 2010). This behavioral pattern shows convergence with other soil-dwelling predators (e.g., spiders and scorpions) that construct vertical burrows, suggesting such traces in continental deposits may reflect recurrent predatory behaviors in the geological record (Hembree 2023). The striking morphological congruence between modern tiger beetle larval burrows and *S. serratus* demonstrates their multifunctional nature, serving simultaneously as domiciles and predation sites (i.e., combined dwelling and feeding behavior). Such burrow complexity is rarely possible to infer only from the fossil record, needing neoichnological studies as a comparative.

The consistency of paleoenvironmental controls in the occurrence of *Skolithos serratus* observed in this study and previous works (Netto 2007, Nascimento & Netto 2019), also for extant tiger beetles can suggest a degree of niche conservatism for riverbanks and floodplains (Pearson & Vogler 2001). Despite the abundance of tiger beetles in modern environments, *S. serratus* remains poorly documented in continental deposits, with only rare occurrences reported (Mángano *et al.* 1994, Netto 2007, Nascimento & Netto 2019). This contrasts with the more frequent preservation of other *Skolithos* ichnospecies (*S. linearis* for example) in similar environments (e.g., Adserà 2018, Sedorko *et al.* 2020). This apparent discrepancy may reflect niche specialization within the *Skolithos serratus* tracemaker. While *Skolithos linearis* is ubiquitous across fluvial environments, including abandoned channels, crevasse splays, and distal floodplains (Melchor *et al.* 2012, Wang *et al.* 2014, Valencia *et al.* 2024), *S. serratus* exhibits a more restricted distribution, limited to habitats with specific substrate textures and moisture conditions.

Despite their broad distribution in continental settings, mostly in fluvial systems, modern tiger beetles display selective oviposition behavior, targeting substrates that facilitate larval burrowing (Pearson 1988, Brust *et al.* 2005).

When combined with ecological constraints like resource availability (Knisley & Pearson 1984), this substrate specificity results in high burrow density within sharply delimited environmental niches. In addition to niche dynamics, the role of substrate properties, especially consistency and plasticity, critically influence trace preservation. These factors determine burrow fidelity and the retention of diagnostic features (e.g., scratch marks), which are directly linked to tracemaker morphology (Savrda 2007).

For *Skolithos serratus*, substrate characteristics are crucial for preserving the typical burrow wall ornamentation with screw pattern. All known occurrences of *S. serratus* in the geological record are associated with heterolithic deposits of fine sand and mud, suggesting that mud content significantly aids preservation of the distinctive scratch patterns on burrow walls. Recent neoichnological studies with mole crickets demonstrate that substrate mud content directly controls both the quality of wall ornamentation preservation and the resulting ichnotaxonomic expression. Sedorko *et al.* (2024) showed that varying mud percentages led mole crickets to produce three distinct ichnogenera during burrowing, highlighting how subtle substrate differences can profoundly impact trace fossil morphology and preservation. Thus, increasing sand content in substrates can result in poorly developed or absent scratch marks (Sedorko *et al.* 2024). Consequently, the low recognition of *Skolithos serratus* in sandy deposits likely reflects a taphonomic bias. The lack of preserved wall ornamentation in coarse-grained substrates may hinder identification, leading to confusion with other ichnospecies, such as *Skolithos linearis*. In sum, the biological preferences and substrate characteristics are the probable responsible for the scarcity of *Skolithos serratus* in the geological record.

5. CONCLUSIONS

The presence of *Skolithos serratus* in the lacustrine Cretaceous Quiricó Formation holds significant ichnological and paleoecological importance, extending the stratigraphic and

environmental range of this ichnotaxon beyond its previously recorded fluvial Triassic occurrences in Brazil. This record also provides an opportunity to discuss the primary controls in their occurrence and preservation. The producer of *Skolithos serratus* colonized exposed deposits during brief periods of stability between depositional events, known as colonization windows. The results further indicate that colonization occurred in well-drained, firm substrates, as evidenced by scratch marks. The exclusive occurrence of *Skolithos serratus* in heterolithic fine-grained substrates suggests an ecological preference of the tracemaker, restricting its distribution to specific portions of the fluvial landscape. Additionally, substrate consistency and plasticity critically influenced the preservation of *Skolithos serratus*, likely explaining its limited records in continental deposits due to taphonomic biases.

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